

# Suspension Feeding by the Lophophore-like Apparatus of the Pterobranch Hemichordate *Rhabdopleura normani*

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**Abstract.** Selective forces acting on feeding mechanisms have played an important role in the evolution of metazoans. To develop a more accurate understanding of the evolution of feeding within the deuterostome and lophophorate clades, I used video analysis and electron microscopy to examine suspension-feeding behavior and ciliation patterns in *Rhabdopleura normani*, a pterobranch hemichordate. In *R. normani*, local reversals of ciliary beat capture food particles, and the normal feeding activity does not involve the use of mucus to capture particles. Also, several different methods of particle rejection are identified. Lateral, frontal, and frontolateral ciliary bands, which are composed of cilia 8–13  $\mu\text{m}$  in length, are present on the tentacles. In *R. normani* from Bermuda, ciliated perforations occur along the length of the arms, specifically between the bases of adjacent tentacles. These structures are previously undescribed in suspension-feeding organisms. My findings are consistent with the hypothesis that the tentaculated arms of pterobranchs are homologous to the lophophores of brachiopods, phoronids, and bryozoans. The similarities in the feeding biology of these groups are discussed.

## Introduction

The course of evolution within a taxon can be greatly influenced by selective forces on feeding mechanics and morphology. The classic examples of the Cichlidae (Liem, 1973) and Darwin's finches (Darwin, 1972; Grant, 1986) demonstrate that major shifts in diet and food acquisition

can occur in a relatively short time. Feeding morphology and methods of feeding may also be correlated with the origin and divergence of phyla. To determine whether this is the case, I am analyzing the evolution of feeding within the deuterostome and lophophorate clades. Because information about the feeding of both deuterostome and lophophorate taxa is essential to this analysis, this paper will focus on pterobranch hemichordates.

Pterobranchs are a class of marine hemichordates that suspension feed with ciliated tentacles. Unfortunately, our knowledge of pterobranch feeding biology is very limited. Gilmour (1979) and Stebbing and Dilly (1972) provided some observations on the feeding of living *Rhabdopleura compacta*, and Lester (1985) commented on *Cephalodiscus gracilis* feeding. In the pterobranch *Rhabdopleura normani*, I examined the flow of water around the tentacles, the method of particle capture, methods of particle rejection, and the ciliation pattern of the tentacles. Because some workers assert that the pterobranch feeding apparatus is homologous to the lophophore of brachiopods, bryozoans, and phoronids (Hyman, 1959; Gilmour, 1979; Hoverd, 1985; Lester, 1985; Dilly *et al.*, 1986; Nielsen, 1987), my findings are compared to reports on these taxa (Strathmann, 1973; Gilmour, 1978). There are several similarities between these groups, including patterns of ciliation, use of ciliary reversal in particle capture, similar rejection mechanisms, and similar morphologies.

*R. normani* is a colonial sessile organism that lives on the underside or protected regions of hard substrates (*e.g.*, rocks, coralline rubble, concrete slabs). The entire adult animal is approximately 3 mm in length with tentaculated arms that are 1.5 mm long. A coenecium is secreted by the cephalic shield which also serves a locomotory func-

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tion similar to a molluscan foot. The individuals within the coenecium occupy separate compartments but are connected by an organic stolon. *R. normani* in Bermuda is found in shallow water areas (1–10 m in depth) that are characterized by high flow and limited particulate matter content.

### Materials and Methods

I collected *Rhabdopleura normani* from subtidal areas by free diving under The Causeway bridge in Bermuda, and transported them to Bermuda Biological Station for Research for subsequent observation (see Lester, 1988, for a description of the Bermudan *R. normani*). Feeding was observed with a Wild dissecting scope and a Panasonic video camera. Zooids were examined both within, and removed from, their tubes. Because the zooids were very sensitive to vibrations, I also observed individuals relaxed in a 1:1 mixture of 7.5% MgCl<sub>2</sub> and filtered seawater. This method of relaxation had no noticeable effect on ciliary function or mechanics. Zooids were fed a combination of carbon particles and calcium carbonate particles that varied in size from 10 to 200 μm and were easily ingested. I also used the algae *Dunaliella tertiolecta* (approximately 4 × 10 μm) and *Tetraselimis chuii* (approximately 7 × 13 μm) to track particle movement and capture. Particle motions were also recorded on video tape so that they could be assessed more accurately.

For microscopy, several specimens were relaxed and preserved in either one-third strength Bouin's fixative or 1% glutaraldehyde. Scanning electron microscopy (SEM) specimens were post-fixed with 2% osmium tetroxide, dehydrated in ethanol, and transferred to 2,2-dimethoxypropane before being critical-point dried in carbon dioxide. The specimens were then sputter coated with a gold palladium alloy, and observed with a JEOL-JSM35 scanning microscope. TEM specimens were post-fixed in 2% osmium tetroxide, dehydrated in ethanol, and transferred to propylene oxide before being embedded in an Epon-Araldite mixture. A Siemens Elmiskop IA transmission microscope was used to examine thin sections, and standard light microscopy techniques were used with thick sections.

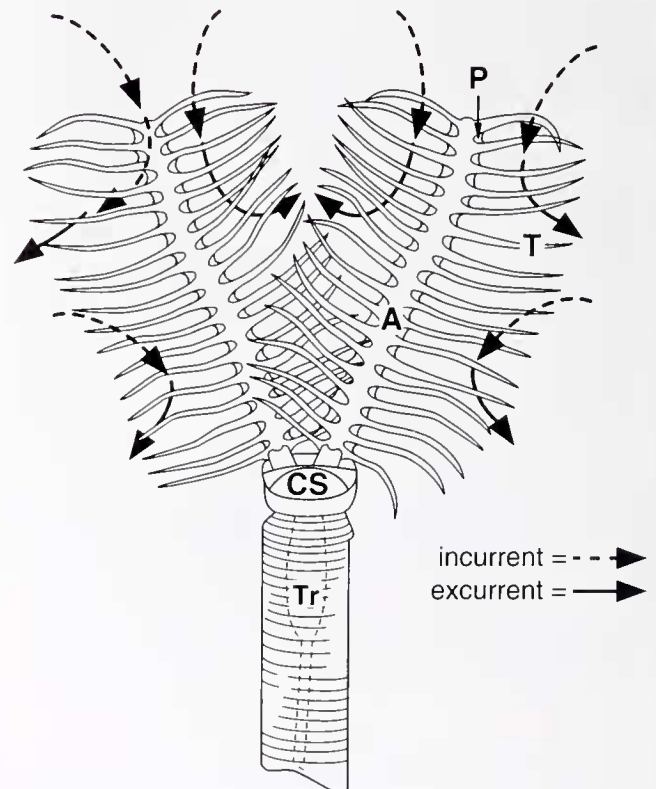
### Results

The suspension-feeding apparatus of *R. normani* consists of numerous tentacles attached to each of two arms. Depending on the contractile state of the zooid, the arms of average mature zooids range from 500 to 1500 μm in length, and 45 to 120 μm in width. The tentacles are 200–500 μm in length and 10–15 μm in diameter. A commissure of tissue connecting adjacent tentacles near their bases (further described below) creates a series of perforations along the length of the arm. To feed, the zooid moves to

the tube aperture, primarily by means of the cephalic shield, and then perches on the rim of the aperture with the anterior lobe of the cephalic shield overhanging the rim of the tube. The role of the cephalic shield in feeding is unclear, but the dense ciliation on the dorsal surface of the shield suggests its involvement in particle manipulation near the mouth. The zooid extends the two feeding arms in line with the tube (*i.e.*, straight extension), but several individuals were observed to curl their arms posteriorly. Once extended, the arms were spread slightly to form a 30–35° angle when viewed from the frontal surface of the arm (Fig. 1). The tentacles are extended such that the profile of an arm viewed end on is V-shaped. Individuals not treated with MgCl<sub>2</sub> showed active tentacle flicking behavior. I was not able to ascertain whether this behavior was involved in either particle rejection or particle capture.

### Morphology

Both SEM and light microscopy reveal four distinct bands of cilia running longitudinally along each ten-

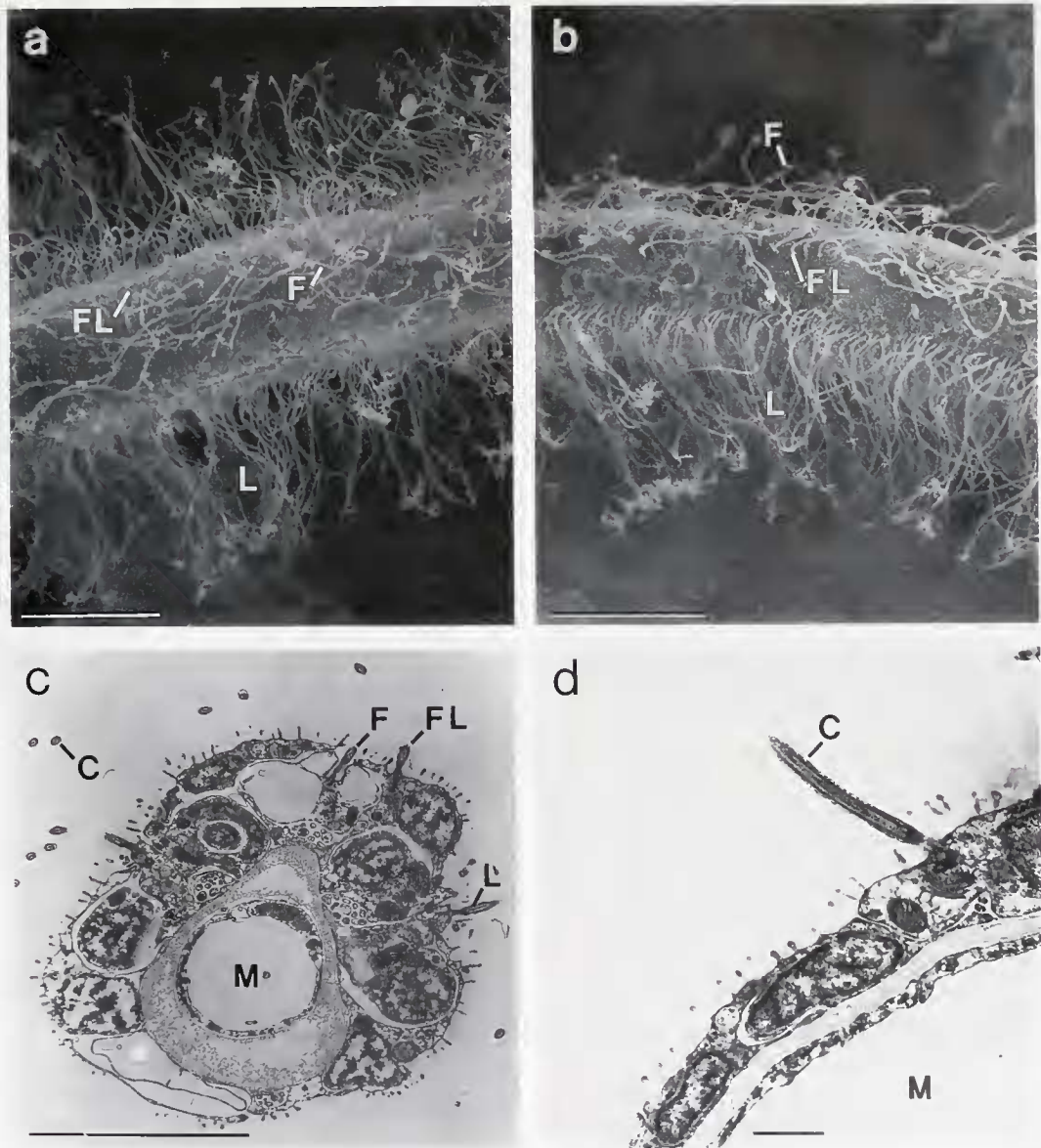


**Figure 1.** The gross morphology and the feeding position of a zooid is shown from an anterior perspective (the arms are topologically dorsal). The tentacular apparatus consists of two main parts, tentacles and arms. The general incurrent flow of water across the feeding apparatus passes from the frontal ciliated surface of the arms and tentacles to the abfrontal surface. The water is then moved posteriorly away from the apparatus as excurrent flow. Broken arrows depict unfiltered water and solid arrows depict filtered water. A—arm, CS—cephalic shield, P—perforation, T—tentacle, Tr—trunk.

tacle. Prominent lateral cilia, 10–13  $\mu\text{m}$  in length, make up two of the ciliated bands (Fig. 2a). My findings confirm Nielsen's (1987) report that these bands are composed of two rows of monociliated cells. Two additional rows of single cilia are present in the frontolateral position of the tentacles (Fig. 2b). These cilia are slightly shorter, about 8–10  $\mu\text{m}$ . Finally some sparse frontal cilia (8–10  $\mu\text{m}$ ) are also present. There are no ciliated tracts on the abfrontal surface of the tentacle. All three types

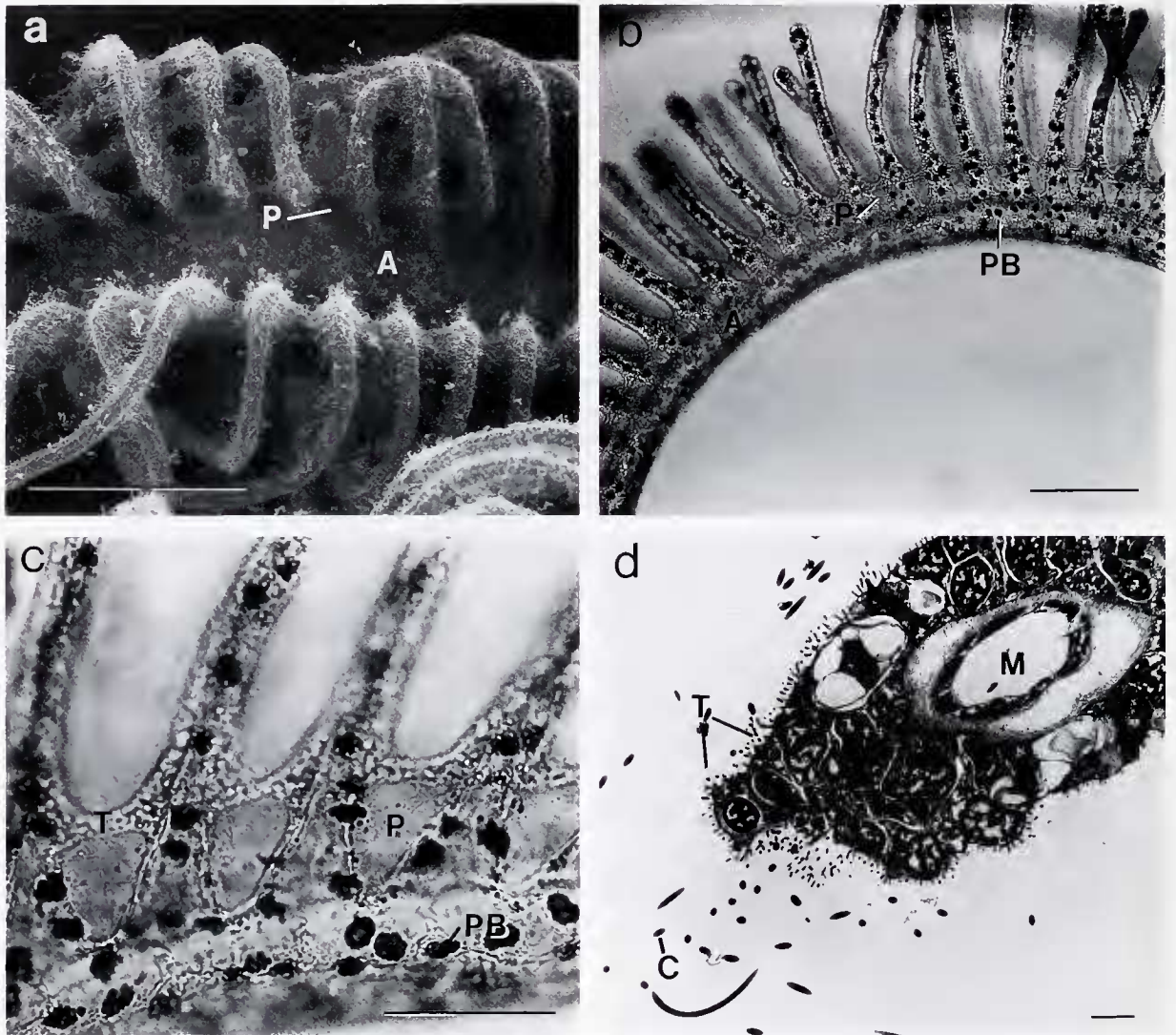
of ciliated bands are represented in Figure 2c, which is a TEM of a tentacle in cross-section. Microvilli completely cover the tentacle as well as the frontal surface of the arm (Fig. 2d). My findings corroborate those of Gilmour (1979) in *R. compacta* and Dilly *et al.* (1986) in *Cephalodiscus gracilis*.

The frontal surface of the arms is densely ciliated throughout its length (Fig. 3a). I was not able to discern whether these cilia formed one large ciliated



**Figure 2.** Ciliation patterns on the tentacle and arm of *Rhabdopleura normani*. (A) SEM of tentacle in frontal view reveals the ciliary pattern (scale bar = 10  $\mu\text{m}$ ). (B) SEM of tentacle in lateral view (scale bar = 10  $\mu\text{m}$ ) (C) TEM of tentacle in cross section (scale bar = 10  $\mu\text{m}$ ). A frontal and a right frontolateral cilium are shown, but the corresponding left frontolateral cilium is not. (D) TEM of the arm in cross section showing the frontal surface. Note the numerous microvilli (scale bar = 1  $\mu\text{m}$ ). C—cilium, F—frontal cilia, FL—frontolateral cilia, L—lateral cilia, M—mesocoelom.





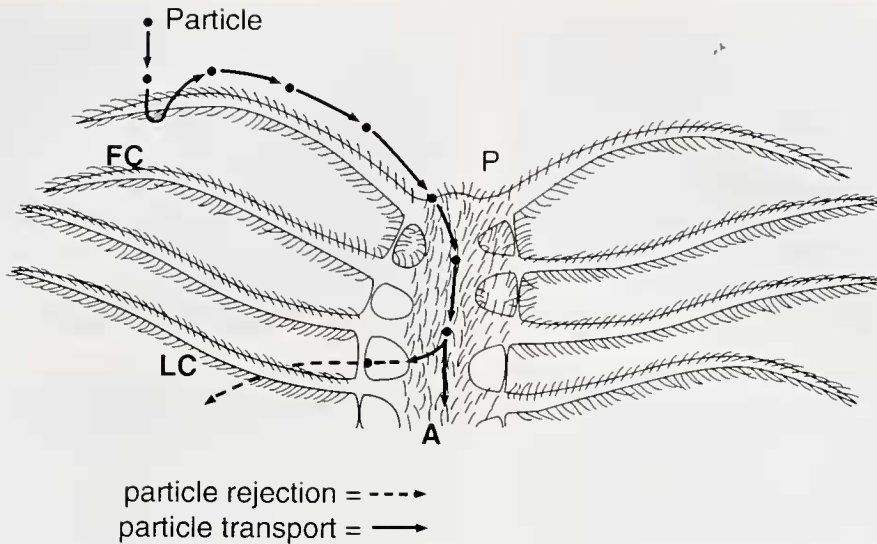
**Figure 3.** Perforations at the base of the tentacles. (A) A frontal view of the arm (SEM) showing the dense ciliation and the ciliated perforations between the bases of the tentacles (scale bar = 100  $\mu$ m). (B) A light micrograph of an arm viewed from the side showing the distribution of the pigmented bodies and the location of the perforations (scale bar = 100  $\mu$ m). (C) A light micrograph of the ciliated perforations at high magnification (scale bar = 50  $\mu$ m). (D) A tentacular cross section (TEM) that partially includes the tissue bridge delimiting the perforation. Cross sections of cilia along the length of the bridge are also obvious (scale bar = 1  $\mu$ m). A—arm, C—cilium, P—perforation, PB—pigmented body, M—mesocoelom, T—tissue commissure.

tract or several smaller ciliated fields. Because of their orientation when viewed with the SEM and light microscope, the cilia were difficult to measure; nevertheless, they appeared to be about 10–12  $\mu$ m in length.

Perforations are present between the bases of adjacent tentacles and are formed by a commissure of tissue that connects the tentacles (Fig. 3b). These perforations are 10–25  $\mu$ m in height and 10–14  $\mu$ m in width (Fig. 3c). The commissure that delimits the distal por-

tion of each hole is composed of cellular components (Fig. 3d) and cilia are present along the rim of the aperture. Presumably, the flow of water around the arm and tentacle bases is affected by this series of perforations.

Dark pigmented bodies (Fig. 3b, c) and cilia are distributed over the entire epidermis of *R. normani*. These bodies are especially visible in the tentaculated region where the surrounding tissue is translucent, but their function and composition are not known.



**Figure 4.** Particles are captured by local reversal in beat of the lateral cilia. Particles are then transported down the tentacle to the arm by the frontal and frontolateral cilia. Once on the arm, the particle can be rejected through one of the perforations, or sent to the mouth for ingestion. Note: in this diagram, the number of cilia on the feeding apparatus has been reduced to increase the clarity. A—arm, FC—frontal and frontolateral cilia, LC—lateral cilia, P—perforation.

### Feeding

The direction and position of water currents generated by the zooids were determined as follows. Small colonies of zooids,  $\leq 10$  cm in diameter, were placed in eight-inch finger bowls with standing filtered seawater. Zooids removed from their tubes were treated in a similar manner, but no more than 10 individuals were examined in a four-inch finger bowl or a 15-mm petri dish. Particles were added to the water distal to the arm and above the frontal tentacular surface of a mature zooid in normal feeding posture. The movement of the particles was indicative of the flow of water near the feeding apparatus. In both intact zooids and zooids removed from their tubes, the water currents generated by the metachronal beating of lateral cilia are toward the frontal ciliated surface of the arms and tentacles, between and perpendicular to the tentacles, and then away from the zooid's abfrontal tentaculated surface (Fig. 1). Even though a current produced by the frontal surface of the ciliated arm is not obvious, observations of particle capture, particle transport, and ciliation suggest that a current is generated down the length of the arm in a distal-to-proximal direction.

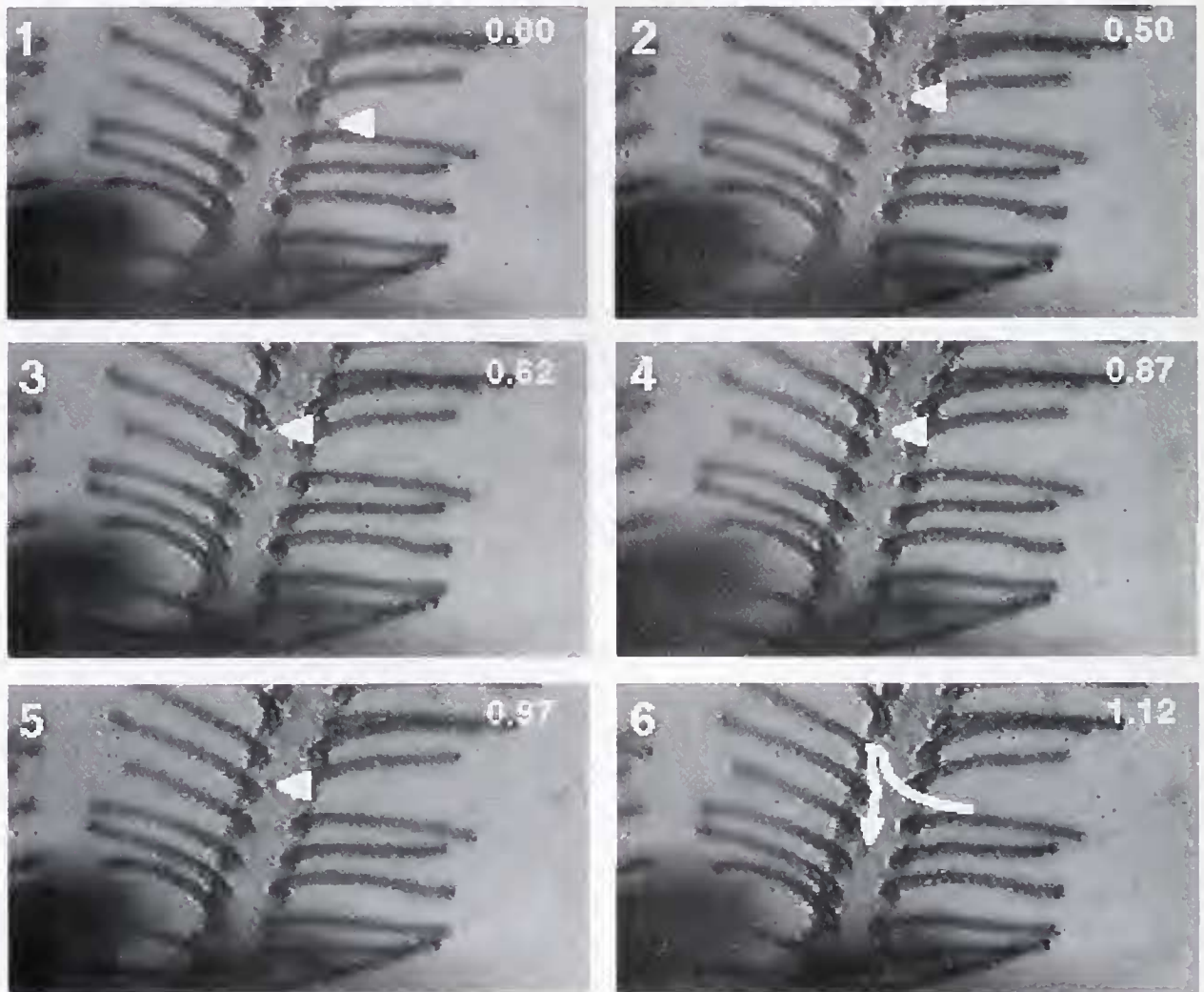
The particles captured by zooids ranged in size from 9 to 70  $\mu\text{m}$ , but additional work is needed to determine the size range of particles that are actually ingested. As the water currents carry the particles between the tentacles, lateral cilia capture the particles and transfer them to the frontal side of the tentacle. In several cases, the particles captured are seen to change or reverse direction abruptly and bounce onto the frontal surface of the tentacle. This

observation indicates that some particles are captured by a local reversal of beat by the lateral cilia and not by impingement on the cilia (see Hart, 1991, for a more detailed description of particle capture by ciliary reversal). Once on the frontal surface, the particle is transported down the length of a tentacle by the frontolateral and frontal cilia, then quickly transferred to the ciliated tract of the arm, and transported down the arm directly to the mouth (Fig. 4). Particle transport on the arm is perpendicular to and much more rapid than that on the tentacles. There is no evidence of mucus in normal feeding (*i.e.*, during particle capture and transport down the tentacles and arms), and the independent motion of particles further suggests that mucus is not used.

Figure 5 shows a video montage of a particle being captured by ciliary reversal near the base of a tentacle. While this particular event did not occur further out on the tentacle, as is typical (see Fig. 4), the abrupt change in particle direction indicative of ciliary reversal is evident. However, observing a capture by ciliary reversal is dependent upon the angle at which the particle path is viewed; *i.e.*, the degree with which a particle changes direction is determined by the viewing angle.

To control for this bias, two categories of observation for particle capture are scored. In both cases, the mechanism of particle capture is ciliary reversal. The first category is characterized strictly by a change of  $\geq 90^\circ$  in the particle's path. Using this criterion, ciliary reversals are observed to occur in 19.9% of all capture events by the entire feeding apparatus, and 23.5% of captures by the





**Figure 5.** Ciliary reversal. This figure is a montage of frames taken from a video tape of *Rhabdopleura norman* feeding. The arrow heads point to a particle that is pulled down into the feeding apparatus by water vortices (1–2), contacts a tentacle at the base (3), and then immediately reverses direction and is transported down the tentacle and arm toward the mouth (4–6). The arrow in frame six indicates the particle path. The elapsed time in seconds is shown in the upper right of each frame.

tentacles (Table 1). These observations are highly credible since this criterion for identifying a ciliary reversal event is conservative. Thus, explanation by alternative hypotheses (e.g., impingement on the cilia, sieving by the cilia) can be excluded. The second category of particle captures, which is less restrictive, is defined by a sudden  $30^\circ$  to  $90^\circ$  change in particle direction. Such events occurred in 53.9% of all particle captures and 63.9% of those by the tentacles.

Furthermore, direct observation with a compound light microscope confirmed that the ciliary beat is altered when particles contact the lateral cilia. Individual zooids were placed in a depression slide under the microscope, and algal particles were added. Even though the particle path

could not be accurately followed due to the magnification, when the particle contacted the cilia a change of beat was evident.

In addition to particle capture by the tentacles, the frontal ciliated surface of the arm captures particles directly, though I was unable to determine whether ciliary beat was altered when particles were captured in this fashion. Although direct capture by the arm occurs infrequently, it still accounted for a noticeable portion, 15.6%, of all particles captured.

Thus, the total number of ciliary reversal events (category 1 and category 2) observed was 104 out of 141 capture events, or 73.8% of all observed events. If just the captures by ciliary reversal on the tentacle are analyzed (because

Table I

## Particle capture

	Number of particles captured	% of particles captured	% of particles captured by tentacles
Capture on tentacles by a $\geq 90^\circ$ change in particle's path	28	19.9%	23.5%
Capture on tentacles by a sudden $30^\circ$ to $90^\circ$ change in particle's path	76	53.9%	63.9%
Capture on tentacles by a $< 30^\circ$ change in particle's path	15	10.6%	12.6%
Particle capture on the arms	22	15.6%	—
Total	141		

the occurrence of ciliary reversal during captures by the arms could not be substantiated), 87.4% (104 out of 119) of all tentacular capture events are due to ciliary reversal. In 12.6% of all particle capture events that occurred on the tentacles, ciliary reversals were not observed. Although the captures of these particles may have occurred by ciliary reversal, other mechanistic hypotheses of particle capture cannot be ruled out.

As water passed over the tentacles, the proportion of particles that were captured and the proportion that were ingested varied from near 0% to almost 100%, depending upon particle concentration, particle type, and duration of the feeding experiment. These proportions were lowest when particle concentration was high and when the feeding experiment was long ( $\geq 1$  h). Also, algal particles were more efficiently cleared and more often ingested than the artificial food particles.

The ciliated perforations apparently have no direct function in particle capture. During my analysis, no particles were ever observed to be captured or trapped by the cilia around these perforations and then transported towards the mouth.

## Particle rejection

Particle rejection occurs when a particle is actively captured and released at some point prior to ingestion. In *R. normani*, I observed four types of particle rejection. The data in Table II are representative of *R. normani* feeding, in that the largest category of particles are those ingested, and the four different types of particle rejection mechanisms are observed. Fifty percent of the particles rejected are merely captured on the tentacles, transferred to the frontal side of the tentacle, and then discharged or lost.

Also, the frontal surface of the tentacles can transport large particles distally via the frontolateral and frontal cilia, and expel them at the tentacle tip. This observation, which occurred in 9.7% of the rejections, is consistent with Gilmour's (1979) findings in *R. compacta*. Gilmour also reported that mucus is involved in rejection in *R. compacta*, but water currents quickly carry particles away in *R. normani* and the particles move independently, indicating that mucus is not involved in transport along the tentacles.

In the third type of particle rejection, particles may be lost during transfer from the tentacle to the arm. While I have interpreted this behavior as particle rejection, it might just as easily be seen as an inefficiency in particle transfer.

The last type of particle rejection, accounting for 31.9% of such observations, involves the perforated tentacular structures. As particles are transported down the arm, they may be suddenly shuffled off at a  $45$ – $90^\circ$  angle and released through one of the many perforations found between the tentacle bases. Figure 4 shows a schematic of this event, and Figure 6 shows a video montage of this type of rejection. In observing live animals, the passage of the particle under the tissue commissure and through the perforation can clearly be seen. Because cilia can only beat in one plane, I hypothesize that two types of cilia (*i.e.*, those involved in particle transport towards the mouth, and those involved in particle transport toward the perforations) are present on the frontal surface of the arm to account for this peculiar particle motion.

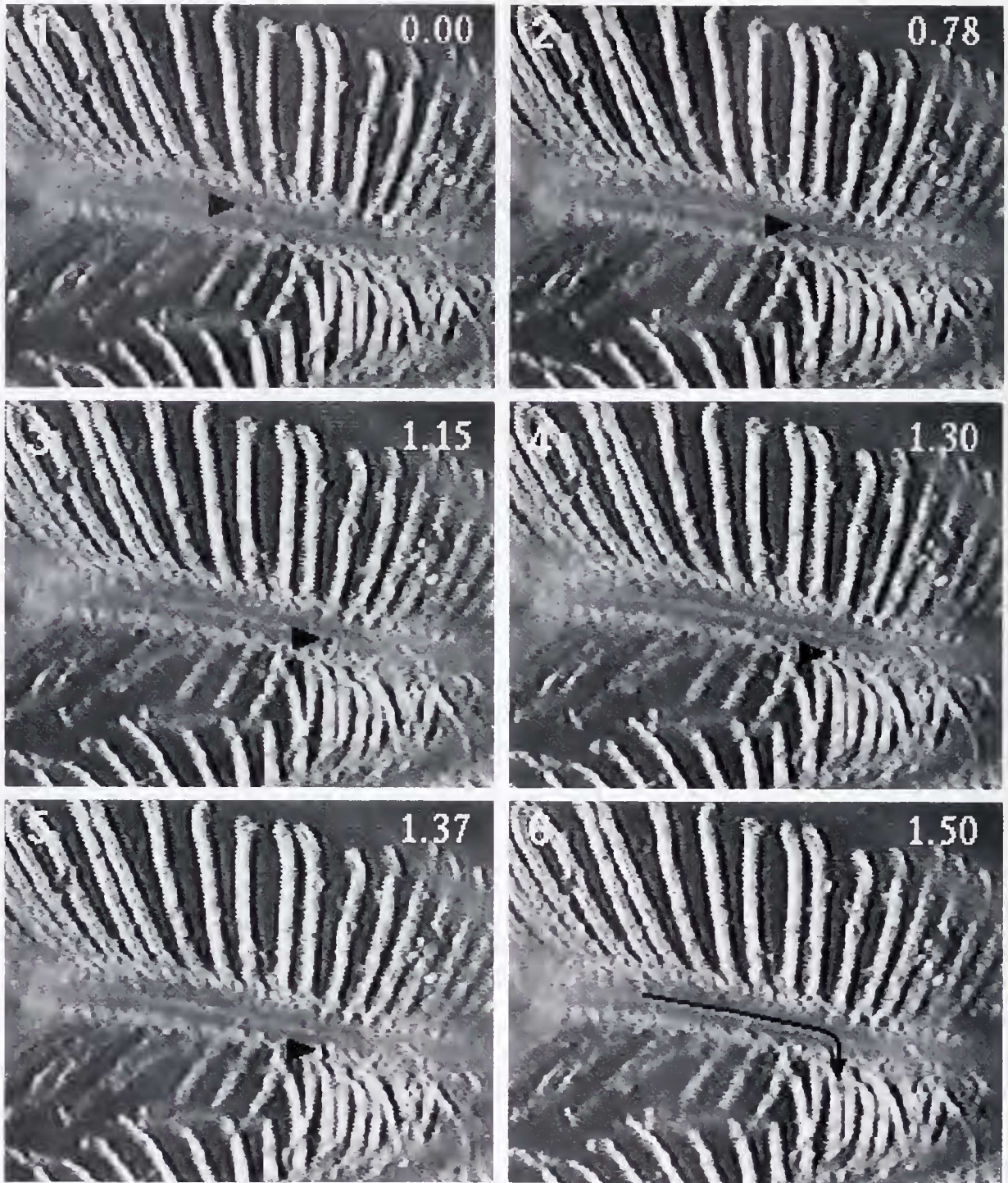
Infrequently, larger particles become lodged in the apertures at the tentacle base. Because this occurs only when zooids are flooded with a high concentration of particles, it may be an artifact. As the concentration of particles presented increases and the fouling of the feeding apparatus occurs, rejection through the perforations and by distal transport of particles along the tentacles accounts for a much greater percentage of particle rejection events. Moreover, when the feeding apparatus is very fouled, particles become stationary temporarily, and the tentaculated

Table II

## Fate of captured particles

	Number of captured particles	% of particles	% of particles not ingested
Ingested	69	48.9%	—
Loss from tentacle	36	25.5%	50.0%
Distal transport off tentacle	7	5.0%	9.7%
Loss during arm-tentacle transfer	6	4.3%	8.3%
Through perforation	23	16.3%	31.9%
Total	141		





**Figure 6.** Particle rejection. The arrowheads in this figure point to a food particle that is traveling down the length of the arm towards the mouth (1-2). The particle abruptly changes direction (3) and is shuffled off at a 90° angle through a perforation (4-6). The arrow in frame six indicates the particle path. The elapsed time in seconds is shown in the upper right of each frame.



arms secrete mucus to facilitate the removal of fouling particles.

### Discussion

#### *Impingement or reversal*

The actual method of particle capture by the lophophorates and other deuterostome groups is currently the source of a controversy in the literature. Are particles captured by an impingement process (Gilmour, 1978, 1979), or is a local reversal of ciliary beat used to capture particles (Strathmann, 1973; Strathmann and Bonar, 1976; Hart, 1991)? Gilmour (1979) and Stebbing and Dilly (1972) both reported that impingement is the main method of particle capture by pterobranchs. However, an impingement hypothesis cannot explain several of my observations. Namely, particles quickly change or reverse direction at angles  $\geq 90^\circ$ , and particles bounce from the lateral cilia to the frontal surface of the tentacle. An impingement hypothesis postulates that such movements should not occur. Furthermore, as Strathmann (1973) has argued, food particles are only slightly denser than the water, so it is doubtful that food particles could cross flow lines with sufficient force to allow impingement on the cilia. Gilmour (1978) has also suggested that impingement is the main mechanism of particle capture in lophophorates, but this is contrary to both my own unpublished data and Strathmann's (1973) observations of these taxa.

The conclusion that a ciliary reversal mechanism is used by pterobranchs is an inference based on particle motion. Previous studies validate such an inference. Using cinefilms, reversal ciliary beats associated with particle capture have been directly observed in pluteus larva of echinoids (Strathmann *et al.*, 1972) and in adult bryozoans (Strathmann, 1982), and I have observed altered ciliary beat in pterobranchs. Also, Hart (1990) pharmacologically manipulated calcium channels to demonstrate that particle capture in echinoderm larvae is dependent on ciliary reversal.

However, an impingement mechanism for particle capture by pterobranchs cannot be completely ruled out. Because only 23.5% of those particles captured on pterobranch tentacles demonstrated obvious ciliary reversal, the use of an impingement mechanism as well is conceivable. When the tentaculated arms were flooded with high particle concentrations and became fouled, particles often appeared "stuck," possibly by impingement on the cilia, and surrounded with mucus. Because this event was observed only when the tentaculated arms were fouled, I interpreted it as a cleaning mechanism and not a particle-capture mechanism.

The distribution of animals that use ciliary reversal extends beyond the lophophorates and pterobranchs. The larvae of enteropneusts (Strathmann and Bonar, 1976)

and echinoderms (Strathmann, 1971; Hart, 1991) use ciliary reversal mechanisms, which, however, have not been identified in protostome organisms. Curiously, the cilia involved in ciliary reversal in these taxa are usually 20–30  $\mu\text{m}$  long compared to the 10–13  $\mu\text{m}$  long cilia of pterobranchs. The use of ciliary reversal to capture food can also be dependent on the life-history stage. For example, ciliary reversal mechanisms have not been demonstrated in adult forms of enteropneusts or echinoderms, and, while ciliary reversal is present in adult bryozoans, the cyphonautes larva uses sieving instead (Strathmann and McEdward, 1986; McEdward and Strathmann, 1987).

#### *Pterobranchs versus lophophorates*

The feeding apparatuses of pterobranchs, brachiopods, bryozoans, and phoronids have several similar attributes (Table III). At a gross morphological level, the feeding structure is a ring of tentacles that surrounds the oral region and is invaded by mesocoelom. This superficial similarity was recognized by early workers who initially allied pterobranchs with the Bryozoa within the "Lophopea" (Allman, 1869).

Table III

#### *Feeding apparatus similarities\**

	Pter	Phor	Brac	Bryo
1) Extensions of the mesocoelom invade the tentacles.	+	+	+	+
2) Lateral, frontal, and frontolateral ciliary bands are present on the tentacles.	+	+	+	+
3) Lateral cilia generate a water current between and perpendicular to the tentacles that draws water from the frontal surface to the abfrontal surface.	+	+	+	+
4) A local reversal of ciliary beat is used to capture food particles.	+	+	+	+
5) Particles are transported by the frontal and frontolateral cilia down the tentacle.	+	+	+	+
6) Mucus is not used in normal feeding activity.	+	+	+	+
7) Particles are rejected by distal transport along the frontal surface of the tentacle.	+	+	+	+
8) Tentacles are innervated.	+	+	+	+/-
9) Tentacles contain blood vessels.	+	+	+/-	-

\* Data obtained from Hyman (1959), Nielsen (1987), Strathmann (1973), Gilmour (1978, 1979), Reed and Cloney (1977), Smith (1973), and my own unpublished results.

But the similarities extend beyond gross morphology to structure and function. In all four taxa, the tentacles have lateral, frontolateral, and frontal ciliary bands (Strathmann, 1973; Nielsen, 1987). The lateral cilia generate a flow of water around the feeding apparatus that draws water from the frontal surface, moves the water between and perpendicular to the tentacles, and then passes it abfrontally away from the feeding apparatus (Strathmann, 1973). In the case of brachiopods, the presence of the valves causes the water current to be redirected after it has passed through the tentacular region. As the water passes between the tentacles, particles are captured with the lateral bands of cilia by a local reversal of ciliary beat. After particle capture, the frontal and frontolateral cilia transport particles proximally down the frontal side of the tentacle without the use of mucus.

The particle-rejection mechanism, in which large particles are moved distally along the tentacles, is similar among the lophophorates and the pterobranchs. This particular mechanism often involves the use of mucus in bryozoans, brachiopods, and phoronids (Strathmann, 1973; pers. obs.). Although I did not observe mucus used in this manner under normal conditions, it has been reported in pterobranchs (Gilmour, 1979) and is seen when the tentaculated arms are sufficiently fouled. Additional structural similarities, such as extensions of the blood vascular system and the nervous system into the tentacles, have been observed in the pterobranchs, phoronids, and brachiopods (Hyman, 1959; Dilly *et al.*, 1986; Halanych, unpub.).

Earlier workers (Hyman, 1959; Gilmour, 1979; Hoverd, 1985; Lester, 1985; Dilly *et al.*, 1986; Nielsen, 1987) postulated a possible homology among the tentacles of pterobranchs and the lophophore, and my findings are consistent with that notion. Furthermore, whereas any one of the above characteristics may be found in other suspension-feeding organisms (*e.g.*, polychaetes), the entire suite of characters (nos. 1–7 in Table III) is unique to pterobranchs, phoronids, brachiopods, and bryozoans. Without a phylogeny to determine character evolution, one cannot, however, infer whether these commonalities are due to a shared evolutionary history or due to similar selective pressures on sessile tentaculated suspension-feeders.

There are two differences between *R. normani* and lophophorates. First, pterobranch cilia are much shorter than those of brachiopods, bryozoans, and phoronids. To confirm this finding I examined *Cephalodiscus gracilis* from the same locality in Bermuda. The cilia of *C. gracilis* are also 10–13  $\mu\text{m}$  long, and I found no cilium longer than 15  $\mu\text{m}$ . Second, the ciliated perforations found in Bermuda specimens of *R. normani* are unique. *C. gracilis* has no similar structures at the base of its tentacles, nor is any similar structure reported in the literature. Although

these structures are used in particle rejection, their effect on flow around the feeding apparatus is unclear.

These differences and similarities between the lophophorates and pterobranchs continue to generate many interesting hypotheses about how evolution has shaped the ability of organisms to acquire food. When the molecular phylogeny of these groups has finally been completed by this and other laboratories, many of these hypotheses can be directly tested, and thus provide a much more lucid understanding of early metazoan evolution.

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